BIOMASS, PRODUCTIVITY AND SOIL FORMATION IN EARLY PRIMARY SUCCESSION ON SAND DUNES, S. SWEDEN

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Abstract

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The effects of changes in growth and productivity in ageing vegetation on litter accumulation and soil formation, are studied in a coastal sand dune succession in SE Sweden. The study includes the two earliest stages in the present-day succession, the Ammophila- and Calluna vegetation.

In Ammophila the highest yearly production, both above and below ground, occurs immediately after the dune has reached its final height. After that the yearly peak biomass decreases, and after ca 10 years the peak biomass is about one third of the original. The length of life, especially of the leaves, however, increases with the age of the vegetation. Thus the loss of vigour of the Ammophila, viz. the decrease in yearly peak biomass, with age of the vegetation, can be partly explained as being a redistribution of the use of assimilates within the plants, from producing biomass to maintaining a gradually increasing biomass.

In Calluna vegetation the age structure and the above ground biomass do not change from year to year, due to adventitious rooting of decumbent shoots. Organic matter accumulates on the soil surface for approximately 50 years, after which decomposition equalizes the litter supply.

The concentration of hydrogen ions, bound to the soil exchange positions, is considered to be an indicator of the cation exchange capacity of the soil. It increases linearly with the increasing content of humus, by ca 30 μmoles$\cdot$(g humus)$^{-1}$. This proves the importance of humus in the soil for the cation exchange capacity.

The accumulation of organic matter with age of the vegetation implies a corresponding accumulation of nitrogen in the dead organic material. In Ammophila, as well as in Calluna, there is an accumulation of nitrogen in the biomass, until 90% of the total nitrogen is in the dead biomass, and 10% in the living parts. At this point an equilibrium is reached, where the release of nitrogen, either in decomposition residues, or in a mineralized form, in the underlying soil horizons equals the supply through the litter formation.

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The thesis includes the following papers:

A. Changes in structure and function of Ammophila during primary succession. - Oikos 34 (in press).
B. Structure and dynamics of Calluna vulgaris on sand dunes in South Sweden. - Oikos 35 (in press).
C. Soil development and nitrogen accumulation in two coastal sand dune ecosystems. - Meddn. Växekol. Inst., Lunds Univ. 41.

The papers will be referred to by the above Capital letters.

INTRODUCTION

The aim of the present study is to quantify changes in productivity and biomass in a primary succession, and to relate this to litter accumulation and soil formation. The study has been carried out in the sand dune area at Sandhammaren ($55^{\circ}23'$ N, $14^{\circ}12'$ E), S. Sweden, and includes the two earliest discernible stages in the present-day succession within the area, the Ammophila- and Calluna vegetation. The study has mainly been restricted to mapping the changes in growth and productivity in ageing vegetation within this sand dune succession, from newly colonized Ammophila arenaria (L.) Link and A. baltica (Flugg) Link vegetation, to the old Calluna vulgaris (L.) Hull heath. The effects of these changes on the rate and pattern of accumulation of organic matter in and on the soil, will be summarized in a simple model. The effects of the organic matter on the soil chemical processes, as indicated by the soil pH and turnover of nitrogen, will be discussed.

BIOMASS AND PRODUCTION

A decline in above ground net productivity with age of the vegetation is shown in Ammophila (A). During the first ten years the yearly net production decreases approximately according to the following equation:

$$P_i = - 120 \, {}^{e}\log i + 400$$

viz. the amount of above ground biomass produced in the tenth year is roughly one third of that, produced in the first year. The below ground growth is shown to decrease approximately in the same manner. During the same period the yearly peak biomass increased by ca 50%, mainly due to a definite increase in the below ground biomass during the first years after colonization. I have thus concluded that the main reason for the decrease in productivity with age of the vegetation is a successively increasing biomass, and thereby an increasing use of assimilates for respiration. Furthermore it shows that the decrease in assimilating biomass in the Ammophila vegetation from year to year is not necessarily followed by a decrease in the gross productivity. The above ground biomass, particularly the leaves, has a longer life span on the old dunes, than on the young ones, which may partly compensate for the year by year decrease in peak above ground assimilating biomass.

The decrease with age in the above ground annual net production - apparent in loss of vigour of the Ammophila vegetation - is consequently not necessarily combined with a loss in gross productivity, but with a redistribution of the use of assimilates within the plants. An important consequence of this is the concomitant change in microenvironment. The increasingly sparse vegetation is increasingly sensitive to wind erosion, and new niches are created which other plants can invade: at Sandhammaren Corynephorus canescens (L.)PB on slightly eroded spots with sand movements in the soil surface, and Calluna vulgaris on places with unbroken soil surface with a distinct, humus-rich uppermost soil layer.

The age structure of the Calluna shoots on three heaths of different ages and at different distances from the shore, do not differ significantly (B). I have concluded that the common cyclical growth pattern in Calluna vulgaris on these sites is replaced by a continuous rejuvenation of the above ground shoots through continuous adventitious rooting of decumbent shoots. This rejuvenating process is dependent on an extremely slow rate of litter decomposition, which gives rise to a fast embedding of the decumbent stems.

The constant age composition is assumed to result in an approximately constant annual net production. The method for measuring net above ground production is therefore based upon differences in mean weight between the different age groups of the shoots.

The continuous rejuvenation of the above ground biomass occurs in a phase of development, which is characterized by high specific competitiveness. The vegetation cover is dense, and has a relatively high productivity, excluding the invasion of other species.

ACCUMULATION OF ORGANIC MATTER

The soil accumulation of organic matter (in the A_{oo}, A_o and B horizons), may be expressed as the sum of all previously produced material, minus the material that has disappeared. The accumulation is in this way dependent on two main variables, supply and loss, varying according to time, amount of litter left, and the degree of decomposition. In Ammophila the supply of litter, viz. the annual net production, decreases with the age of the vegetation according to a logarithmic course (A). The loss of litter is composed of two variables: removal by wind, and decomposition. The wind-removal is assumed to decrease linearly during ten years in proportion to the age of the vegetation. After ten years no removal by wind takes place. The rate of decomposition of

litter is assumed to decrease exponentially with an increasing degree of decomposition. In Ammophila the half-life of the litter is 10-12 years, in Calluna it is 12-14 years. The model for accumulation applied to the Ammophila vegetation (A), results in a maximum accumulation of organic matter in the soil surface of about 1000 g m^{-2} in ca 15 yr old vegetation. After that period the decomposition exceeds the yearly supply of litter, mainly as a consequence of the continuously decreasing annual net production, and the amount of organic matter in the soil surface begins to decrease. In the Calluna sites the supply of litter to the soil surface is considerably greater than in the Ammophila sites (B), partly due to the approximate constant annual production, and partly due to the fact that much of the below ground material is produced in the rawhumus-layer (the A_o), viz. on the former mineral soil surface. This, combined with a slower decomposition rate results after about 50 years in a maximum accumulation of organic matter on the mineral soil surface, which is about ten times greater than the maximum accumulation in Ammophila. The approximate constant production in Calluna also means that, in time, the supply and loss of litter become equal, and the amount of organic matter accumulated remains constant.

As the continuous rejuvenation of the Calluna-vegetation is a function of a continuous excess of litter supply (B), the successive equalization between supply and loss may, in the long run, imply a successive dissolution of the age structure, and thereby create new niches for competing species. The same relation is shown in the Ammophila vegetation (A). The dunes are colonized by i.a. Calluna vulgaris at the time, when the supply and loss of litter are equal.

SOIL DEVELOPMENT

The mineral matter, aeolian sand (median diameter 0.2 mm), is too coarse to be active in the ion exchange processes. The successive accumulation of humus in the soil is therefore of fundamental importance to the soil chemical properties, as all soil exchange activity is due to colloidal humus particles. This is demonstrated in the decreasing pH with age and the increasing humus content in the soil (C). The difference between the concentration of potassium chloride - extractable, and water-extractable hydrogen ions, interpreted as the amount of hydrogen ions bound to the exchange positions, is linearly correlated with the content of humus in the soil. Approximately 30 µmoles hydrogen ions are bound per g humus. As probably the degree of base saturation is very low in all soils in the area, the concentration of fixed hydrogen ions is a rough measure of the relation between cation exchange capacity and humus content in the soil.

The content of nitrogen in the living Ammophila biomass does not change considerably during the first ten years. The decline above ground is compensated by the increase below ground. In the litter there is, however, an accumulation, until about 90% of the total amount of nitrogen is in the dead organic matter, and ca 10% is in the living parts. This stage is reached after 10-15 years, when a total of ca 60 g m^{-2} has accumulated, and the supply of nitrogen to the biomass is balanced by a loss through decomposition. In the Calluna stands the same ratio between nitrogen in living and dead biomass respectively is valid as in Ammophila. In this case the supply and loss become equalized when ca 80 g m^{-2} has accumulated. At that stage the supply through the approximate constant litter production is balanced by a loss downwards in the soil in the form of decomposition residues, and nitrogen continues to accumulate deeper down in the soil.

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